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Published in:
Plant ecology

DOI:
10.1023/A:1013239805915

Plant Ecology **155:** 119–127, 2001.

Effects of introduction and exclusion of large herbivores on small rodent communities

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Received 22 January 2001; accepted in revised form 20 February 2001

Key words: Grazing introduction, Herbivory, Seed survival, Vegetation structure, Woodland dynamics

Abstract

In this study we analysed the effects of large herbivores on small rodent communities in different habitats using large herbivore exclosures. We studied the effects of three year grazing introduction by red deer (*Cervus elaphus* L.) in previously ungrazed pine and oak woodland and the exclusion of grazing by red deer, roe deer (*Capreolus capreolus* L.) and mouflon (*Ovis ammon musimin* L.) in formerly, heavily grazed pine woodland and heathland. At eight exclosure sites within each habitat type, small rodents were captured with live traps using trapping grids. At each trapping grid, seed plots of beechnuts (*Fagus sylvatica* L.) and acorns (*Quercus robur* L.) were placed to measure seed predation by rodents. Exclusion of grazing by large herbivores in formerly, heavily grazed habitats had a significant effect on small rodent communities. Inside exclosures higher densities of mainly wood mice (*Apodemus sylvaticus* L.) and field voles (*Microtus agrestis* L.) were captured. Introduction of grazing by red deer appeared to have no significant negative effects on small rodent communities. The seed predation intensity of beechnuts and acorns by small rodents was significantly higher in ungrazed situations, particularly in habitats that were excluded from grazing. The differences between grazing introduction and exclusion effects on small rodent communities can be explained by differences in vegetation structure development. The recovery of heavily browsed understory vegetation after large herbivore grazing exclusion proceeded faster than the understory degradation due to grazing introduction. Small rodents depend on structural rich vegetations mainly for shelter. We conclude that large herbivores can have significant effects on vegetation dynamics not only via direct plant consumption but also through indirect effects by reducing the habitat quality of small rodent habitats.

Introduction

The direct effects of large mammalian herbivores on the vegetation composition and dynamics have been widely studied. Herbivores affect the vegetation through biomass removal (Pacala and Crawley 1992; McInnes et al. 1992; Harper 1977) but also modify vegetation structure through physical disturbance. The effects of herbivory on vegetation structure depend on habitat type, herbivore species and grazing pressure (Olff and Ritchie 1998). In heathlands, a heavy grazing pressure of red deer and sheep can induce a decrease in plant height and architecture of heather which may result in a short vegetation of graminoids and forbs (Welch and Scott 1995). Severe browsing by red deer (*Cervus elaphus* L.) and moose (*Alces alces* L.) in woodlands may eventually eliminate the shrub layer and prevent tree regeneration (Putman et al. 1989; McInnes et al. 1992).

The indirect effect of herbivory on vegetation structure, is an underestimated phenomenon. By modifying the vegetation structure large herbivores may indirectly affect small herbivores such as small rodents and their predators (Putman 1986). Small rodents occur at high densities in structurally complex habitats with high cover of ferns (den Ouden and Smit 1997), bramble (van Apeldoorn et al. 1990), grasses (Foster and Gaines 1991) or juvenile trees (Hazebroek et al. 1995). Small rodents depend on the shelter in these habitats which provides protection against

predators (Miller and Getz 1976; Hansson 1978), suitable microclimates and profitable food resources (Keesing 1998).

Small rodents can have significant effects on vegetation dynamics. Especially via seed predation and dispersal of tree seeds, small rodents can have a major impact on the establishment of tree species and thus on vegetation succession (Vander Wall 1990; Jensen 1982). We hypothesise that grazing by large herbivores will induce a decrease in small rodent densities due to a decrease in structural complexity of the vegetation. Consequently, large herbivores will induce lower seed predation due to reduced small rodent densities. In this study we try to determine the effects of large herbivores on small rodent communities and seed predation in a spatial mosaic of habitat types in different stages of vegetation succession and with a different grazing history. We studied the indirect effects of grazing by (i) measuring rodent densities and (ii) predation of tree seeds, within and outside large herbivore exclosures.

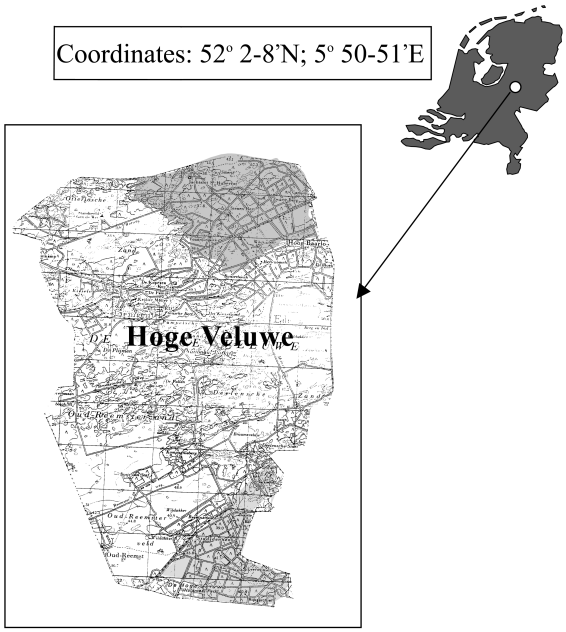

Figure 1. The location of the National Park 'The Hoge Veluwe' in the Netherlands and the spatial position of the exclusion area (unshaded) consisting of heathlands and first generation pine woodlands and the introduction area (shaded) recently available to large herbivores, consisting of second generation pine and oak woodlands.

Methods and materials

Study area

The study was conducted in The National Park 'De Hoge Veluwe' in the Netherlands (52° 2–8′N; 5° 50–51′E) during October – December 1996 (Figure 1). The park comprises a typical landscape on sandy soils of glacial and inter-glacial origin. The climate in the area is oceanic with mean annual temperatures of 9.1 °C and annual rainfall of 800 mm (Krijnen and Nellestijn 1992). The National Park has a long history of grazing by large herbivores. Since their introduction around 1900 red deer, mouflon (*Ovis ammon musimon* Schreber) and wild boar (*Sus scrofa* L.) occur in varying numbers. Roe deer (*Capreolus capreolus* L.) occurs naturally in the park. The mean annual densities of large herbivores based on spring counts in 1999 are 230 red deer, 230 mouflon, 200 roe deer and 50 wild boar. Hunting controls these numbers. Until 1993 the populations of red deer, mouflon and wild boar were concentrated in a central, enclosed area of 3800 ha. In November 1994, the area available to these populations was expanded to 5000 ha.

The major habitat types in the area are assumed to be part of a successional sequence (Fanta 1982) (Table 1). Early successional stages feature heather (*Calluna vulgaris* L.) dominated vegetation communities on driftsand and blown-out plains with grey hair-grass (*Corynepherus canescens* L.) and sheep's fescue (*Festuca filiformis* Pourr.) followed by first generation Scots pine dominated vegetation with an understory (< 50 cm) of sand sedge (*Carex arenaria* L.) and wavy hair-grass (*Deschampsia flexuosa* L.). Following these stages comes second generation Scots pine with an understory of blue berry (*Vaccinium myrtilis* L.) and a shrub layer of rowan (*Sorbus aucuparia* L.) and silver birch (*Betula pendula* Roth.). Late successional species like common oak (*Quercus robur* L.) and beech (*Fagus sylvatica* L.) dominate the deciduous woodlands. Heathland and first generation pine woodland are situated inside the formerly, heavily grazed game area and have been grazed since 1900 by red deer, roe deer and mouflon while second generation pine woodland and oak woodland became available to red deer and mouflon in November 1994 (Figure 1).

Experimental design

In 1994, 32 exclosures of 15 × 25 m excluding all large herbivores including rabbits, were placed to monitor changes in vegetation composition with and

Table 1. Habitat type description (Nomenclature follows Meijden van der (1996))

Habitat type	Grazing history	Exclusion (E) Introduction (I)	Vegetation	No. hectares in the park
Heathland	> 1900	E	*Calluna vulgaris* *Corynepherus canescens* *Festuca filiformis*	1300
Pine woodland I	> 1900	E	*Pinus sylvestris* *Carex arenaria* *Deschampsia flexuosa*	2000
Pine woodland II	> 1994*	I	*Pinus sylvestris* *Vaccinium myrtilis* *Sorbus aucuparia* *Betula pendula*	600
Oak woodland	> 1994*	I	*Quercus robur* *Fagus sylvatica*	300

* Before 1994 only with roe deer

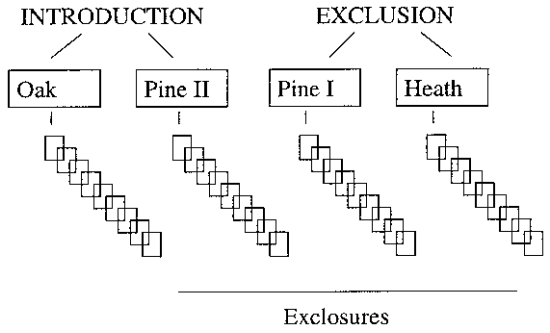

Figure 2. Experimental design divided into an introduction and exclusion area comprising respectively oak and second generation pine woodland and first generation pine woodland and heathland habitats. Each habitat encompasses eight exclosures.

without grazing. We placed 16 exclosures both in the previously ungrazed habitats and in the formerly, heavily grazed game area. In both areas, 8 exclosures were located in each of the four habitat types (Figure 2) consisting of heathland and first generation pine woodland in the formerly, heavily grazed game area and oak woodland and second generation pine woodland in the previously ungrazed area. The exclosures were constructed using wire netting with a height of 200 cm and a mesh width of 5 × 5 cm. The mesh width allowed small rodents to enter the exclosures.

To sample rodent densities we used trapping grids of 15 Longworth live traps placed in grids of 5 × 3 traps with a distance of 5 m between the traps. The traps were filled with hay and baited with rolled oats, apple and carrot. Per exclosure, three similar trapping grids were used, one inside, one outside at a short distance from the fence (10 m) and one outside at a larger distance (75 m). The distance between the two outside grids was large enough to assess independent rodent populations according to home ranges of dominant rodent species like wood mouse (*Apodemus sylvaticus* L.) and bank vole (*Cletrionomys glareolus* Schreber) (Kikkawa 1964). The rodents were captured during 5 days with a prebait period of two days. Each captured and released rodent was marked by cutting a bit of skin, so that it could be individually recognised after recapture.

Habitat features

We distinguished 7 habitat features at each trapping grid that are considered to be important for small rodents (Miller and Getz 1976; Hazebroek et al. 1995; Hansson 1978). We measured the height of the understory (grasses, forbs and dwarf shrubs < 50 cm tall), the understory cover (% cover) and the number of (living) small tree stems with a diameter < 10 cm. Furthermore, we recorded the litter depth (cm), the number of (living) big tree stems (tall trees: diameter > 10 cm), the number of stumps/trunks and dead wood cover (% cover).

Each feature was recorded inside the trapping grids enlarged with 2.5 m in length and width. In each grid the values of the features were based on 10 random samples. Understory height was measured with a foam disc (diameter 10 cm: weight 7.5 g) with a hole in the middle that drops along a wooden stick until stopping on top of a plant. The number of stems was counted and the percentage cover of the understory and dead wood cover was estimated.

Seed predation

During the week preceding the small rodent trapping a seed predation experiment was conducted. In each rodent trapping grid a seed plot was laid in the centre of the capture grid. The grid was sized 5 × 5 m containing 25 acorns and beechnuts. All seeds were laid down on the litter layer, wearing gloves to prevent human odours. All seed pairs were marked with wooden tooth sticks. All seeds were checked daily, and inspected for signs of rodent activity. Seeds were either consumed on the spot (leaving remnants like shells) or were removed completely. Seed predation was measured during one week. In addition, six random exclosures were monitored twice daily to check for possible effects of other, diurnal active seed predators besides the nocturnal small rodents that we studied (Kikkawa 1964).

Data analysis

To test for differences in effects of large herbivores on small rodent communities in exclusion and introduction areas first rodent densities and second seed predation were analysed. The number of individual rodents trapped (Minimum Number Alive (Krebs 1980)) and the total numbers of captures were used as a measure for rodent density per trapping grid. Differences in rodent densities and interactions between grid and habitat type were tested using a hierarchical three-level, type III ANOVA with habitat type, exclosure and trapping grid as factors. The eight exclosures were nested within each of the four habitat types. For analysing respectively *introduction* and *exclusion* effects of grazing, the ANOVA was used separately for rodent densities in introduction (previously ungrazed habitats) and exclusion (formerly, heavily grazed) areas. Differences in grazing effects between the introduction and exclusion area could not be analysed because of the different habitat types occurring in these areas. The ANOVA was followed by Tukey HSD tests for pairwise comparison of the trapping grids (Sokal and Rohlf 1981). Rodent densities were $^{10}\log_{x+1}$ transformed prior to the analysis in order to improve the homogeneity of the data. Prior to the ANOVA, data were checked for normality (Kolmogorov-Smirnov test) and homogeneity (Levene test). Differences in habitat features were tested between grids, using one way ANOVA followed by Tukey HSD tests. Bivariate correlation analysis (Pearson: two-tailed) was used to find out relations between rodent density and habitat features. We only selected habitat features for this analysis that showed significant differences between grazed and ungrazed situations using One Way Anova with Tukey HSD test. Seed predation was measured as the time (number of days) where after seed predation took place, which is reported as the 'survival time' of a seed. Seed survival of acorns and beechnuts was analysed for each seed plot using the Kaplan-Meier survival analysis (Kaplan and Meier 1958: SPSS v 6.0 1994). Significant differences in seed survival were compared between seed grids (inside, next to, outside)and species (acorns, beechnuts) for both introduction and exclusion areas using the Log-Rank Mantel-Cox test (Pyke and Thompson 1986). Seeds that were not predated at the end of the experiment were treated as seeds with survival time equal to the duration of the experiment (seven days).

Results

Rodent density

Overall, only in the exclusion area analysis of variance showed significant differences in rodent density between the trapping grids ($F_{2,28} = 3.96$, $P = 0.031$). A significant higher rodent density inside exclosures as compared to outside and next to trapping grids was measured (Table 2). The rodent densities (total number of individuals & captures) in the introduction area did not differ significantly between the trapping grids. In the exclusion area, the rodent density varied greatly over the habitat types (total number of individuals: $F_{1,28} = 8.71$, $P = 0.01$; total number of captures: $F_{1,28} = 7.81$, $P = 0.01$) with higher rodent densities in pine woodland as compared with heathland. Within the habitat types no significant differences in rodent densities between the trapping grids were found.

Rodent species

In general, wood mouse was the dominant rodent species (Table 2), whereas field voles (*Microtis agrestis* L.) and bank voles were present in lower numbers. Wood mice were caught in all habitat types (Figure 3) while field voles were more common in heathland and first generation pine woodland and bank voles in second generation pine woodland and oak woodland. The wood mice density (total number of individuals)

Table 2. Averages and standard errors of the mean of rodent densities (n=16) per trapping grid, per grazing area (*Introduction* and *Exclusion* area).

Species	INTRODUCTION						EXCLUSION					
	inside	s.e	next to	s.e	outside	s.e	inside	s.e	next to	s.e	outside	s.e
Total individuals	6.63	0.92	5.75	0.93	7.06	1.00	5.56 [a]	0.96	4.56	0.98	3.38	0.83
Total captures	15.13	2.47	11.25	2.34	15.38	2.54	12.25 [b]	2.16	8.25	2.02	7.25	1.76
Total individuals	5.31	0.66	5.06	0.71	6.00	0.75	5.06 [a]	0.90	4.19	0.92	3.25	0.82
Apodemus Sylvaticus												
Total captures	10.69	1.49	8.63	1.26	12.56	1.88	10.25	2.07	7.38	1.71	7.13	1.76
Apodemus Sylvaticus												
Total individuals	0.13	0.13	0.00	0.00	0.06	0.06	0.50	0.22	0.38	0.18	0.13	0.09
Microtis agrestis												
Total captures	0.69	0.69	0.00	0.00	0.06	0.06	2.00 [a]	1.00	0.88	0.54	0.13	0.09
Microtis agrestis												
Total individuals	1.19	0.57	0.88	0.44	1.00	0.41	0.00	0.00	0.00	0.00	0.00	0.00
Clethrionomys glareolus												
Total captures	3.75	1.94	2.63	1.47	2.75	1.26	0.00	0.00	0.00	0.00	0.00	0.00
Clethrionomys glareolus												

Significantly different at $\alpha = 0.05$ according to Tukey HSD test. [a] = significantly different between inside – outside, [b] = significantly different between inside – outside & inside – next to.

in the exclusion area differed significantly between the trapping grids ($F_{2,28} = 3.81$, $P = 0.03$; Table 2) and habitat types ($F_{1,28} = 9.82$, $P = 0.007$). Also, the field vole density (total number of captures) in the exclusion area was significantly higher inside exclosures as compared to outside exclosures ($F_{2,28} = 3.41$, $P = 0.04$; Table 2).

Habitat features

There were no significant differences in habitat features between the trapping grids when all 32 exclosures were taken into account (Table 3). When the formerly, heavily grazed exclosures were considered separately, we found a significant higher understory height inside than outside exclosures (Tukey HSD: $F_{2,47} = 3.28$, $P = 0.047$). We selected understory height as main habitat variable influenced by grazing to be correlated with rodent density. The difference in understory height between inside and outside grids showed a significantly positive correlation with the difference in total small rodent individuals ($p = 0.40$, $n = 36$, $P < 0.05$) for all exclosures.

Seed predation

At the end of the measurement period 80.8% of all beechnuts and acorns was predated. The vast majority of the seeds were removed (78.8%). Only 2% was gnawed or consumed at the spot. The remaining 19.2% remained untouched. We did not find significant differences in the percentage of these types of seed predation between the seed grids (inside, next to, outside), seed species (beechnuts and acorns) or habitat types. In respectively 91% and 89% of the beechnuts and acorns seed predation took place by night.

The seed survival pattern differed significantly among grazed and ungrazed seed grids for beechnuts as well as acorns in both introduction and exclusion areas (Figure 4). According to the Log rank test, the seed survival times of beechnuts and acorns were significantly higher in the grids outside the exclosures as compared to the grids inside and next to the exclosures (beechnuts: Log Rank statistic (LR): inside = 120.7, outside = 126.5: $P < 0.000$; acorns: LR inside = 89.51, outside = 90.59: $P < 0.000$). Differences in seed survival between the seed species and between the grids inside and next to the exclosures between the exclusion and introduction area were not significant. In heathland, the surival times were significantly higher than in the other habitat types (LR 50.4: $P < 0.000$). Approximately 60% of beechnuts and acorns in the grids next to and inside exclosures survived from predation as compared to approximately 80% in the grids outside exclosures.

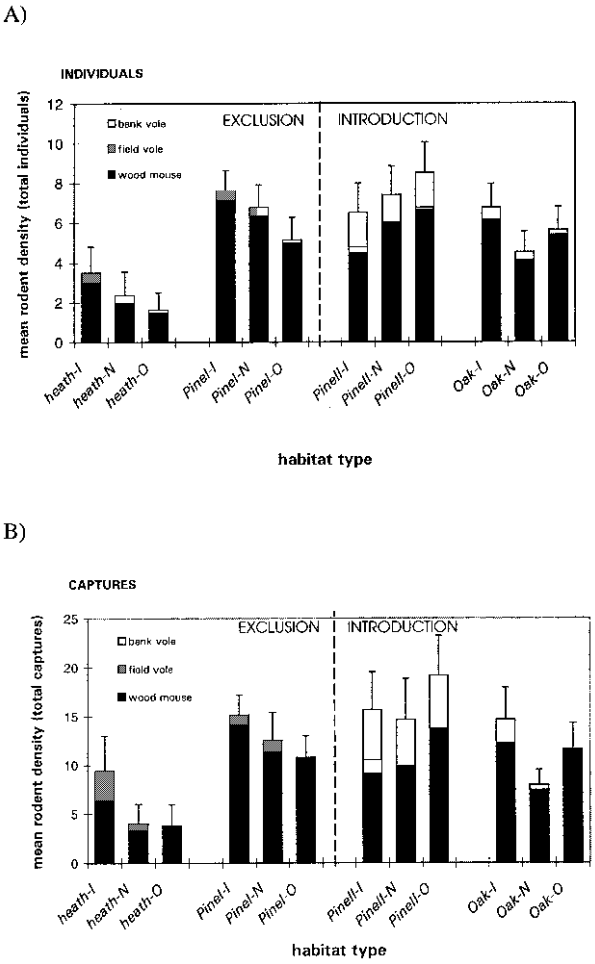

Figure 3. Mean rodent density per species per habitat type inside (i), next to (n) and outside (o) exclosures. A) Total of captured individuals, B) Total number of captures. Vertical lines represent standard errors of the mean.

Rodent density and seed survival

A negative lineair relation was found between wood mice density and the mean survival time of seeds (Figure 5), for acorns: $R^2 = 0.31$, $P < 0.01$, $n = 64$) for grids inside and outside exclosures. A higher wood mice density resulted in a lower mean survival time of acorns.

Discussion

Both our trapping experiment as well as our seed predation experiment pointed out the negative effects of grazing by large herbivores on small rodent communities. First, on the whole rodent densities appeared to be lower outside large herbivore exclosures than inside. Second, rodent densities appeared to be significantly higher inside large herbivore exclosures in the exclusion area. The effects of respectively exclusion and introduction of large herbivores on small rodent communities differed severely. Large herbivore exclusion in heavily grazed habitats had a clear, positive impact on rodent density, while in the presence of large herbivores the rodent density was low. These results confirm the general hypothesis that large herbivores reduce the habitat quality of small rodents and thereby cause a decrease in small rodent density (Geier and Best 1980; Putman 1986; Keesing 1998). Large herbivore exclosures 'create' ideal habitat patches for small rodents in a short, heavily grazed vegetation. Inside exclosures in habitats with a long grazing history a well-developed herb- and shrub layer can recover which provides an appropriate hab-

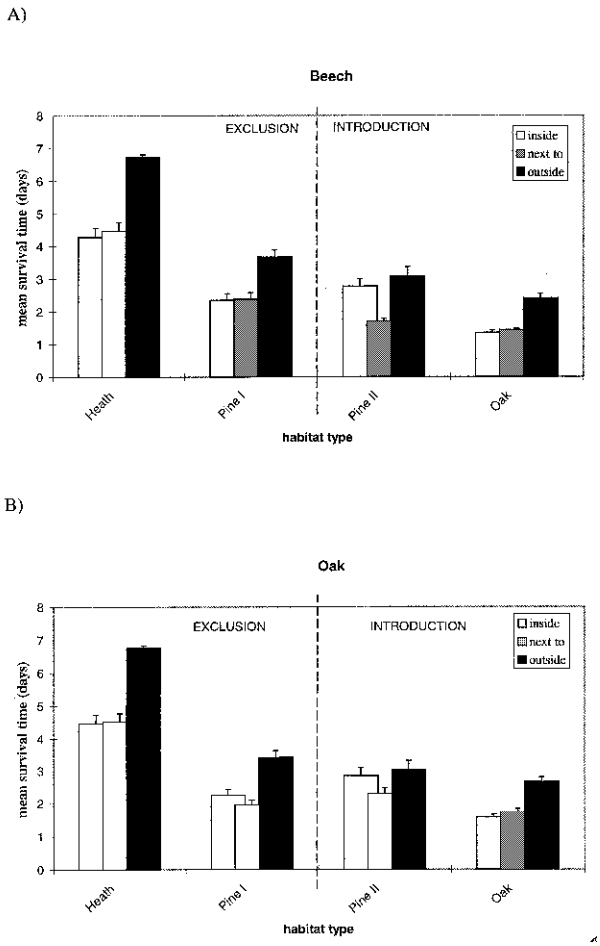

Figure 4. Mean survival times per habitat type inside, next to and outside exclosures for beechnuts (A) and acorns (B).

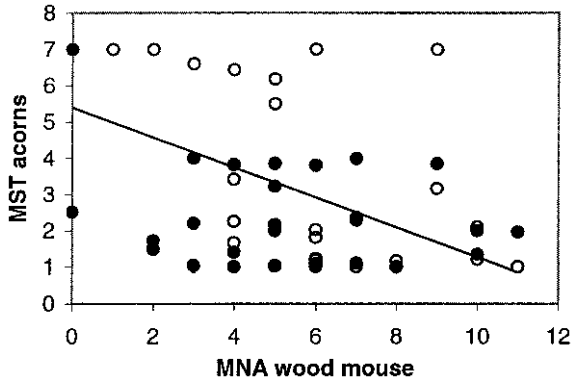

Figure 5. Linear relation between wood mice density (total number of individuals) and mean survival time of acorns for grids inside and outside exclosures in exclusion (open circles) and introduction area (closed circles). $y = -0.42x + 5.4$ $R^2 = 0.31$, $n = 64$, $P < 0.01$.

itat for rodents (Dueser and Shugart 1978; den Ouden and Smit 1997). In our study the vegetation height appeared to correlate significantly with rodent density; a higher vegetation height may imply a better habitat for rodents. Small rodents benefit from a closed understory canopy inside exclosures through a lower apparent predation risk (Kotler 1984; Kotler and Blaustein 1995). Furthermore, the increase of vegetative biomass may also cause an increase in quantity and quality of food availability (Keesing 1998). The recovery of browse-sensitive plant species inside large herbivore exclosures appeared to be fast. We found a fast recovery of mainly rowan in pine woodland, where after three years of grazing release from mainly red deer, approximately 80% of individuals of rowan moved from the smaller (< 50 cm) into the higher (200–500 cm) height classes (Smit, unpub. data). Anderson and Katz (1993) found an apparent recovery of browse-sensitive trees like hemlock (*Tsuga canadensis* L.) after twelve years of white-tailed deer (*Odocoileus viriginianus* Zimmerman) ex-

clusion, while Putman et al. (1989) found a rapid regeneration of birch, beech, oak and holly (*Ilex aquifolium* L.) after 6 years of exclusion of red, roe and fallow deer (*Dama dama* L.) and domestic stock. In fact, exclosures for large herbivores in heavily grazed vegetations become enclosures for small rodents.

The effects of the introduction of large herbivores on rodent communities were not significant. Probably, the actual 3 years of grazing by mainly red deer (Smit et al. 1998) is too short to cause a degradation of the understory and thereby causing a decline in rodent density. Putman et al. (1989) found clear differences in rodent density between large herbivore grazed and ungrazed woodlands after 22 years of grazing, as a result of changes in many habitat features. In general, degradation of vegetation structure by introducing large herbivores may take longer than the recovery of vegetation structure after excluding large herbivores. The selective foraging by large herbivores on the one hand, and the strong recovery capacity of browse-sensitive plants on the other, causes severe differences in vegetation structure development among habitat types which are respectively introduced to and excluded from large herbivores.

In general, large herbivores significantly affect the seed predation by small rodents. Outside the large herbivore exclosures the survival time of acorns and beechnuts appeared to be higher than inside exclosures. Similar to the differences between rodent densities, seed survival differed more distinctly in the exclusion area as compared to the introduction area. Wood mouse, as the dominant small rodent species in our study area and typical granivore species (Watts 1968) appeared to be the main seed predator. A higher wood mouse density caused a lower seed survival. Besides a lower predation risk inside exclosures, small rodents may suffer from a higher exploitation (direct) competition with other seed predators like deer and wild boars (Herrera 1995). In our study area large herbivores and small rodents are sharing food resources. Exclusion of one species (large herbivores) resulted in an increase of the abundance of the other (small rodents) which may refer to direct competition (Schoener 1983; Heske and Brown 1994).

The consequences for vegetation dynamics of the relationship between large herbivores and small rodents are yet unclear. A change in small rodent density can have significant effects on seed dispersal, seed - and seedling survival of woody plants (Ostfeld and Canham 1993). The establishment of seedlings and saplings of oak and beech trees depends on the dual relationship with small rodents. Not all seeds predated by small rodents have to be 'killed' (Price and Jenkins 1986); small rodents can act as dispersal agents. Undiscovered seed caches of small rodents can be recruitment foci of seedlings (Vander Wall 1990; Herrera 1995). The dispersal of heavy seeds of late successional tree species like common oak and beech by wood mice is an important mechanism in forest succession (Jensen 1986; Finegan 1984). According to Janzen (1970) seeds of oak and beech have the best perspectives to escape from seed predators far away from the parent trees. First, seeds have to be hoarded by rodents to reach 'safe sites' (Harper 1977) and second, seeds need a temporary low small rodent density to ensure seed survival and subsequent seedling establishment.

Acknowledgements

We wish to thank the National Park 'De Hoge Veluwe' for allowing access in the park and conducting this study; especially B. Boers and B. Snijders, H. Olff, E.S. Bakker, F. Berendse, M. Gleichman, M. E. Ritchie, R. Ostfeld, R. Virtanen and R. J. Putman for helpful comments during the writing of this manuscript. We are grateful to N.W.O and the Hugo de Vries foundation for financial support.

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